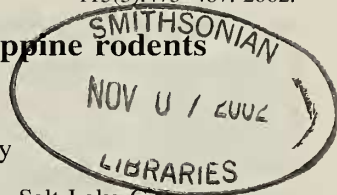


**Further studies on the chromosomes of Philippine rodents
(Muridae: Murinae)**

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Abstract.—Standard karyotypes of ten species of Philippine murine rodents representing seven genera are reported for the first time, and new information is presented for six additional species. Data now available from 25 species (39% of the total Philippine murine fauna) reveal substantial karyotypic diversity, but also show differences among subgroups in the degree of interspecific variability. Within some genera there are major karyotypic differences between species whereas other groups appear to be highly conservative. These data provide only limited information on phylogenetic relationships, but are very useful in clarifying boundaries between groups. In some genera, speciation events apparently have been accompanied by major chromosomal rearrangements. Only a single case is now known of congeneric species having the same karyotype on a single landmass.

As presently understood, the remarkably diverse murine rodent fauna of the Philippines includes 64 species belonging to 23 genera (Heaney et al. 1998). Of these, 55 species (86%) and 16 genera (70%) are endemic to the Philippines, a pattern that reflects relatively few successful colonization events followed by repeated speciation and diversification within this isolated archipelago (Heaney & Rickart 1990). An earlier report on karyotypes of several Philippine murines (Rickart & Musser 1993) revealed substantial diversity in chromosomal characteristics, and provided some support for phylogenetic relationships inferred from morphology.

In this paper, we present new chromosomal data from 16 species of Philippine murines representing 11 genera; this brings the total to 25 species karyotyped from the Philippines. Included are the first reports on chromosomes of three endemic genera (*Celaenomys*, *Limnomys*, and *Tarsomys*), first reports for species in the genera *Apomys*

and *Chrotomys*, and additional information on species reported previously (Rickart & Musser 1993, Rickart et al. 1998). We discuss the significance of this expanded data set within the context of the alternative phylogenetic hypotheses posed by Musser & Heaney (1992).

Methods

Specimens were collected directly from wild populations during field studies conducted in 1988 (on Catanduanes, Luzon, and Negros islands), 1993 (Mindanao Island), and 2001 (Luzon Island). Animals captured in live traps were processed and killed with sodium pentobarbital within 24 h of capture. Cells were prepared from bone marrow and/or spleen tissue following in vivo methodology (Patton 1967, as modified by Rickart et al. 1989). Material from freshly killed animals caught in snap traps was processed in vitro (Rickart et al. 1998). Cells were processed and fixed in the field,

and standard (non-differentially stained) karyotypes were prepared from stored cell suspensions. Giemsa-banded preparations were made for some taxa (Seabright 1971). Determinations of diploid number were based on counts from a minimum of 10 cells per individual. Chromosome terminology follows Rickart & Musser (1993). As used here, fundamental number (FN) refers to the number of major chromosome arms in the entire complement (excluding very minute arms). Because non-differentially stained chromosomes seldom reveal the full extent of variation (Haiduk et al. 1981), differences between standard karyotypes are considered minimal reflections of actual differences, while apparent similarities are interpreted cautiously. Statements regarding possible directions of karyotypic change are based on outgroup comparisons, not on a priori assumptions as to the relative frequency of chromosome fusion vs. fission, or that common arrangements are primitive (Qumsiyeh & Baker 1988).

The sampled taxa are in the subfamily Murinae of the family Muridae, as defined by Musser & Carleton (1993). Specimens examined were prepared as complete skeletons or preserved in fluid and are deposited in the Field Museum of Natural History, Chicago (FMNH), the National Museum of Natural History, Smithsonian Institution, Washington (USNM), and the Philippine National Museum, Manila (PNM). Microscope slides and photomicrograph negatives are housed at the Utah Museum of Natural History, University of Utah, Salt Lake City.

Specimens Examined

Phloeomys cumingi (Waterhouse, 1839).—Catanduanes Island, Catanduanes Province, vicinity of Barrio Summit, elev. 250 m, 13°47'N, 124°19'E, 1 female (PNM specimen, EAR field number 1662).

Batomys salomonseni (Sanborn, 1953).—Mindanao Island, Bukidnon Province, Mount Katanglad Range, 16.5 km S, 4 km E Camp

Phillips, elev. 1,900 m, 8°10'30"N, 124°51'E, 1 female (FMNH 147929).

Batomys granti Thomas, 1895.—Luzon Island, Kalinga Province, Balbalan Municipality, Balbalasang, Magdallao, elev. 1,600 m, 17°28'30"N, 121°04'30"E, 1 male (FMNH 169125).

Archboldomys luzonensis Musser, 1982b.—Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 21.5 km E Naga, elev. 1,350–1,750 m, 13°40'N, 123°22'E, 1 female, 1 male (USNM 573505, 573840).

Archboldomys musseri Rickart et al., 1998.—Luzon Island, Kalinga Province, Balbalan Municipality, Balbalasang, Am-licao, 1,900 m, 17°26'30"N, 121°04'15"E, 1 male (FMNH 169122).

Crunomys suncoides Rickart et al., 1998.—Mindanao Island, Bukidnon Province, Mount Katanglad Range, 18.5 km S, 4 km E Camp Phillips, elev. 2,250 m, 8°9'30"N, 124°51'E, 1 male (FMNH 147942).

Mus musculus castaneus Waterhouse, 1843.—Negros Island, Negros Oriental Province, Silliman Farm, Dumaguete, elev. 5 m, 09°18'N, 123°18'E, 1 female, 1 male (USNM 459896, 459897).

Celaenomys silaceus (Thomas, 1895).—Luzon Island, Kalinga Province, Balbalan Municipality, Balbalasang, Am-licao, elev. 1,800 m, 17°26'30"N, 121°04'15"E, 1 male (FMNH 169132).

Chrotomys whiteheadi Thomas, 1895.—Luzon Island, Kalinga Province, Balbalan Municipality, Balbalasang, Mapga, 1,050 m, 17°28'30"N, 121°04'30"E, 1 male (FMNH 169139).

Rhynchomys isarogensis Musser & Freeman, 1981.—Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 21.5 km E Naga, elev. 1,350–1,750 m, 13°40'N, 123°22'E, 3 males (USNM 573575, 573905, 573910).

Apomys datae (Meyer, 1899).—Luzon Island, Kalinga Province, Balbalan Municipality, Balbalasang, Mapga, 1,050 m, 17°28'30"N, 121°04'30"E, 3 males (FMNH

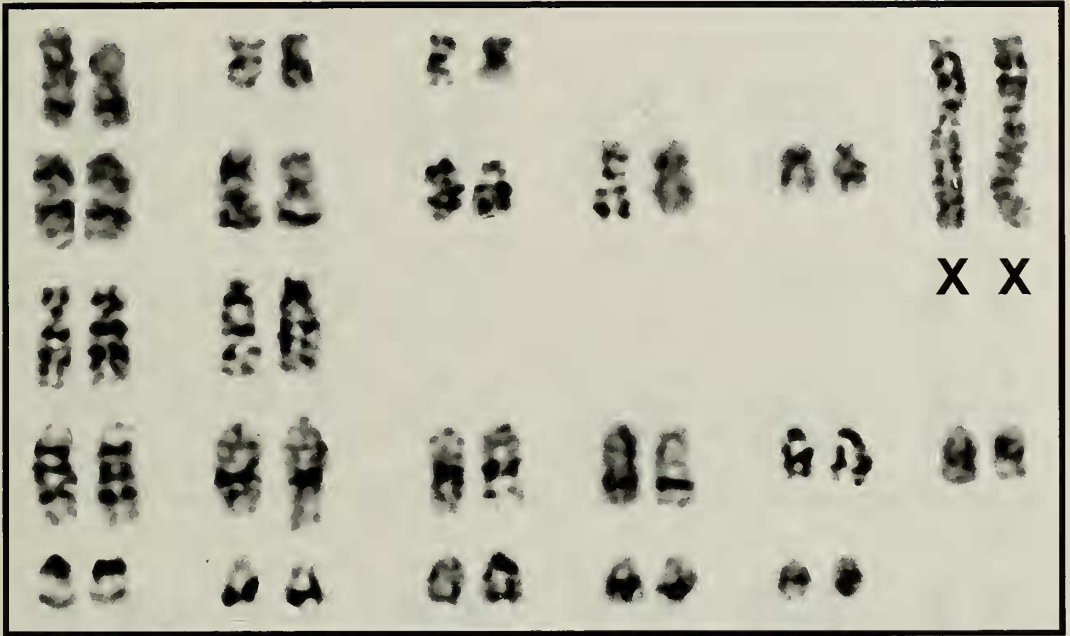


Fig. 1. G-banded chromosomes of *Phloeomys cumingi* female (EAR 1662), $2N = 44$, $FN = 66$.

169051, 169065, 169066), Am-licao, 1,800 m, $17^{\circ}26'30''N$, $121^{\circ}04'15''E$, 1 male (FMNH 169111).

Apomys hylocoetes Mearns, 1905.—Mindanao Island, Bukidnon Province, Mount Katanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1,900 m, $8^{\circ}10'30''N$, $124^{\circ}51'E$, 1 female, 1 male (FMNH 147871, 147872), 18.5 km S, 4 km E Camp Phillips, elev. 2,250 m, $8^{\circ}9'30''N$, $124^{\circ}51'E$, 2 females, 2 males (FMNH 147875, 147878, 147880, 147914).

Apomys insignis Mearns, 1905.—Mindanao Island, Bukidnon Province, Mount Katanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1,900 m, $8^{\circ}10'30''N$, $124^{\circ}51'E$, 1 female, 3 males (FMNH 147912, 147913, 147915, 147916).

Tarsomys apoensis Mearns, 1905.—Mindanao Island, Bukidnon Province, Mount Katanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1,900 m, $8^{\circ}10'30''N$, $124^{\circ}51'E$, 3 males (FMNH 147953, 147955, 147956), 18.5 km S, 4 km E Camp Phillips, elev. 2,250 m, $8^{\circ}9'30''N$, $124^{\circ}51'E$, 1 female, 2 males (FMNH 147957, 147960, 147969).

Limnomys sibuanus Mearns, 1905.—Mindanao Island, Bukidnon Province, Mount Katanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1,900 m, $8^{\circ}10'30''N$, $124^{\circ}51'E$, 1 female, 1 male (FMNH 147944, 147946).

Limnomys sp.—Mindanao Island, Bukidnon Province, Mount Katanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 2,250 m, $8^{\circ}10'30''N$, $124^{\circ}51'E$, 2 males (FMNH 147972, 147975).

Results

Phloeomys cumingi. $2N = 44$, $FN = 66$, Fig. 1.—The standard karyotype of this species, endemic to Luzon faunal region, was described by Rickart & Musser (1993). The autosomal complement includes 8 pairs of metacentric or submetacentric and 11 pairs of telocentric chromosomes. The submetacentric X chromosome is the largest element in the karyotype, and the submetacentric Y chromosome is only slightly smaller. In a G-banded preparation, here reported for the first time, some band patterns

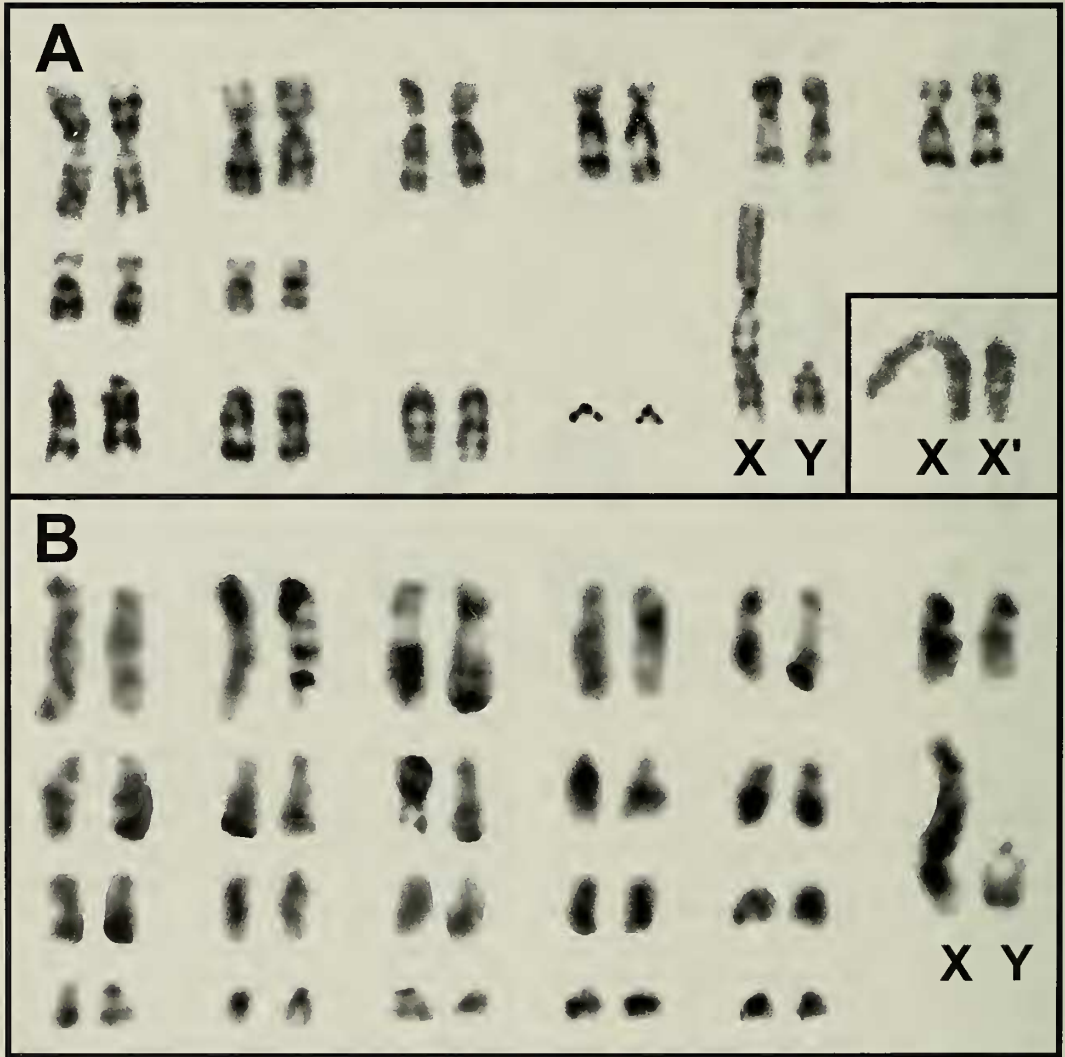


Fig. 2. Chromosomes of: A, *Archboldomys luzonensis* male (USNM 573505), 2N = 26, FN = 43, G-banded preparation, with (inset) sex chromosomes of female (USNM 573840); B, *Archboldomys musseri* male (FMNH 169122), 2N = 44(?), in-vitro preparation from a snap-trapped specimen, identity of sex chromosomes tentative.

are seen on all but the smallest chromosomes allowing most pairs to be matched accurately.

Batomys granti. 2N = 52; FN = 52, not figured.—The karyotype of a specimen of this Luzon endemic from Kalinga Province in northern Luzon consists of 52 telocentric chromosomes, and is indistinguishable from that reported for specimens from Mt. Isarog in southern Luzon (Rickart & Musser 1993).

Batomys salomonseni. 2N = 52, FN = 52, not figured.—The standard karyotype of a specimen from Mindanao appears to be identical to that reported for specimens of this species from Leyte, and is indistinguishable from the standard karyotype of *B. granti* (Rickart & Musser 1993).

Archboldomys luzonensis. 2N = 26, FN = 43, Fig. 2A.—The standard karyotype of this species, restricted to Mt. Isarog in southern Luzon, was described by Rickart

& Musser (1993). The autosomes include 8 biarmed and 4 telocentric chromosome pairs. The submetacentric X chromosome is the largest element in the karyotype, and the Y is small and telocentric. In the one available female specimen, the X chromosome is paired with a large telocentric element. G-banded preparations, here reported for the first time, reveal distinct banding patterns on all autosomes. The long arm of the X chromosome and the large telocentric chromosome of the female appear to have some homologous G-banding. The smaller telocentric Y chromosome also has a distinct band pattern.

Archboldomys musseri. $2N = 44?$; $FN = ?$, Fig. 2B.—A poor-quality in vitro preparation from a male specimen yielded preliminary information on the chromosomes of this species which is restricted to northern Luzon. A diploid number of 44 is estimated for a complement consisting largely of telocentric elements. The X chromosome is tentatively identified as the largest element and the Y chromosome may be a small, telocentric element.

Crunomys suncooides. $2N = 36$, $FN = 36$, Fig. 3A.—Rickart et al. (1998) made a preliminary report on the karyotype of this species, which is known only from Mount Katanglad, Mindanao. Cells from a single male specimen processed in vitro contain 36 telocentric chromosomes. Based on relative size, we tentatively identify the X chromosome as one of the largest elements in the karyotype, and the Y chromosome as one of the smallest.

Mus musculus castaneus. $2N = 40$, $FN = 40$, Fig. 3B.—Specimens of the non-native Asian house mouse from Negros Island have a karyotype of 40 telocentric elements, comparable to those documented for specimens from Thailand (Markvong et al. 1973).

Celaenomys silaceus. $2N = 44$, $FN = 52$, Fig. 4A.—The karyotype of this species, belonging to a monotypic genus restricted to northern Luzon, is here reported for the first time. It includes 2 pairs of small meta-

centric, 1 pair of large submetacentric, 1 pair of large subtelocentric, and 18 pairs of small to large-sized telocentric elements. The X and Y chromosomes cannot be distinguished from the autosomes, but presumably are included within the telocentric series.

Chrotomys whiteheadi. $2N = 38$, $FN = 52$, Fig. 4B.—The karyotype of this species, a northern Luzon endemic, is here reported for the first time. It consists of 2 pairs of small metacentric, 4 pairs of medium to large-sized submetacentric, 1 pair of large subtelocentric, and 12 pairs of small to large-sized telocentric chromosomes. The sex chromosomes are telocentric and cannot be distinguished from the autosomes.

Rhynchomys isarogensis. $2N = 44$, $FN = 52$, not figured.—The karyotype of this species was first described by Rickart & Musser (1993). Reexamination of material from male specimens reveals that the Y chromosome is telocentric rather than submetacentric as reported previously. The standard karyotype is indistinguishable from that of *Celaenomys* (Fig. 4A).

Apomys datae. $2N = 44$, $FN = 54$, Fig. 5A.—This is the first report on the karyotype of this species which is restricted to northern Luzon Island. The autosomal complement includes 5 pairs of small to large-sized biarmed chromosomes and 16 pairs of small to medium-sized telocentric elements. The X chromosome is large and telocentric, and the Y chromosome is small and telocentric.

Apomys hylocoetes. $2N = 48$, $FN = 56$, Fig. 5B.—The karyotype of this species, a Mindanao Island endemic, is here reported for the first time. It includes 1 pair of small submetacentric, 3 pairs of small subtelocentric, and 20 pairs of small to large-sized telocentric chromosomes. Both sex chromosomes are telocentric and cannot be distinguished from the autosomal complement.

Apomys insignis. $2N = 36$, $FN = 72$, Fig. 5C.—This is the first report on the chromosomes of this species which is restricted

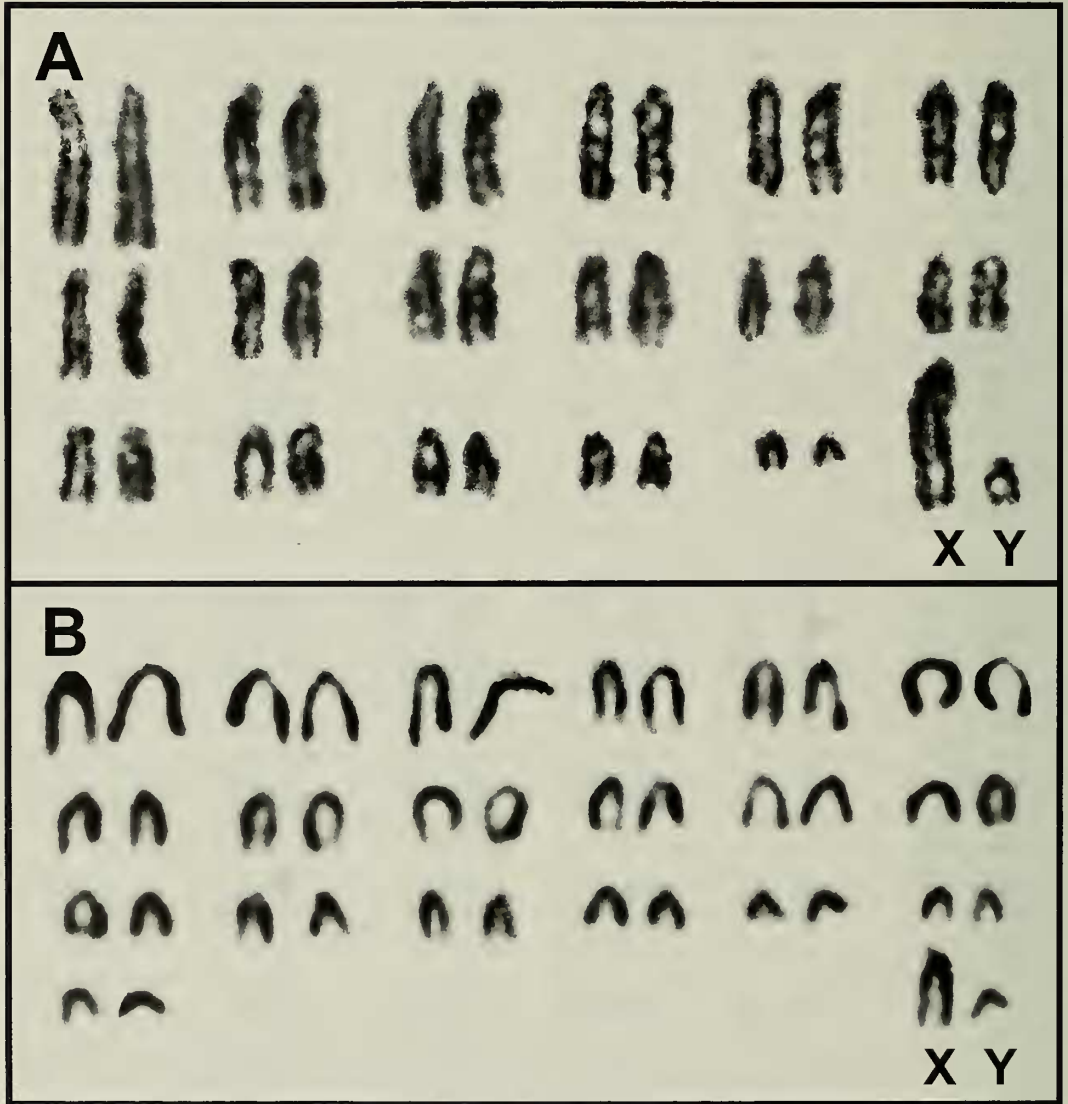


Fig. 3. Chromosomes of: A, *Crunomys suncooides* male (FMNH 147942), 2N = 36, FN = 36, in vitro preparation from a snap-trapped specimen, identity of sex chromosomes tentative; B, *Mus musculus* male (USNM 459896), 2N = 40, FN = 40.

to the Mindanao faunal region. Available material was prepared in vitro from snap-trapped specimens. The karyotype consists entirely of biarmed chromosomes, including 5 pairs of small to large-sized metacentric, 3 pairs of large submetacentric, and 10 pairs of subtelocentric elements. The sex chromosomes cannot be distinguished from the autosomes, but presumably are included within the subtelocentric series.

Limnomys sibuanus. 2N = 42, FN = 61/62, Fig. 6A.—This is the first report on the chromosomes of this species, which is endemic to Mindanao Island. Available material was prepared in vitro from snap-trapped specimens, and quality is relatively poor. The autosomal complement includes 7 metacentric or submetacentric, 2 subtelocentric, and 11 telocentric pairs. The X chromosome is medium-sized and subtelocentric.

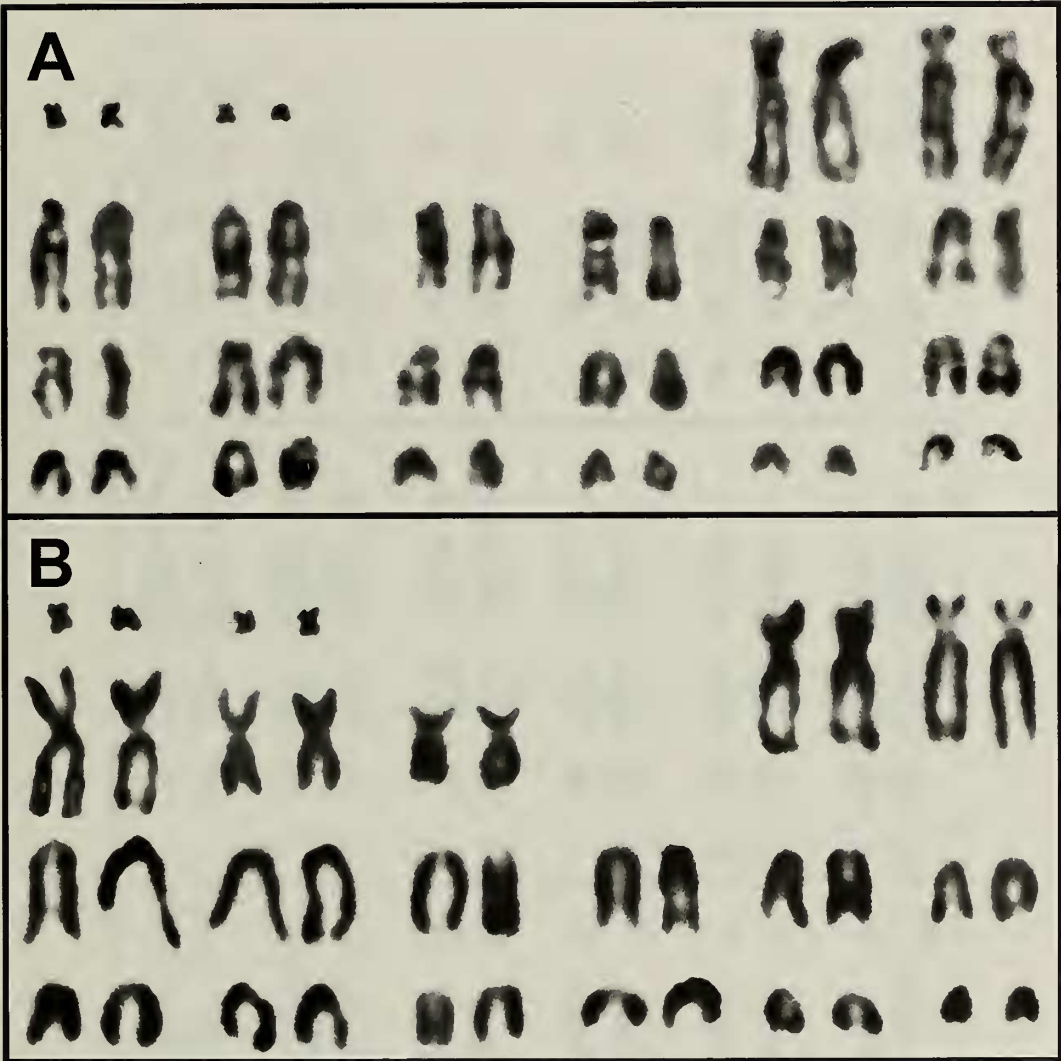


Fig. 4. Chromosomes of: A, *Celaenomys silaceus* male (FMNH 169132), 2N = 44, FN = 52; B, *Chrotomys whiteheadi* male (FMNH 169139), 2N = 38, FN = 52. The sex chromosomes cannot be distinguished from the autosomes in either karyotype.

centric, and the telocentric Y chromosome is the smallest element in the karyotype.

Limnomys sp. 2N = 42, FN = 61/62, Fig. 6B.—The standard karyotype of an undescribed species of *Limnomys* from Mount Katanglad, Mindanao Island, is here reported for the first time. It appears to be identical to that of *Limnomys sibuanus*.

Tarsomys apoensis. 2N = 42, FN = 61/62, Fig. 6C.—The standard karyotype of this species, endemic to Mindanao Island,

is here reported for the first time. The autosomes and the X chromosome appear to be identical to those of *Limnomys*, but the telocentric Y chromosome is substantially larger.

Discussion

In a review of morphological characteristics of Philippine murines, Musser & Heaney (1992) recognized three principal

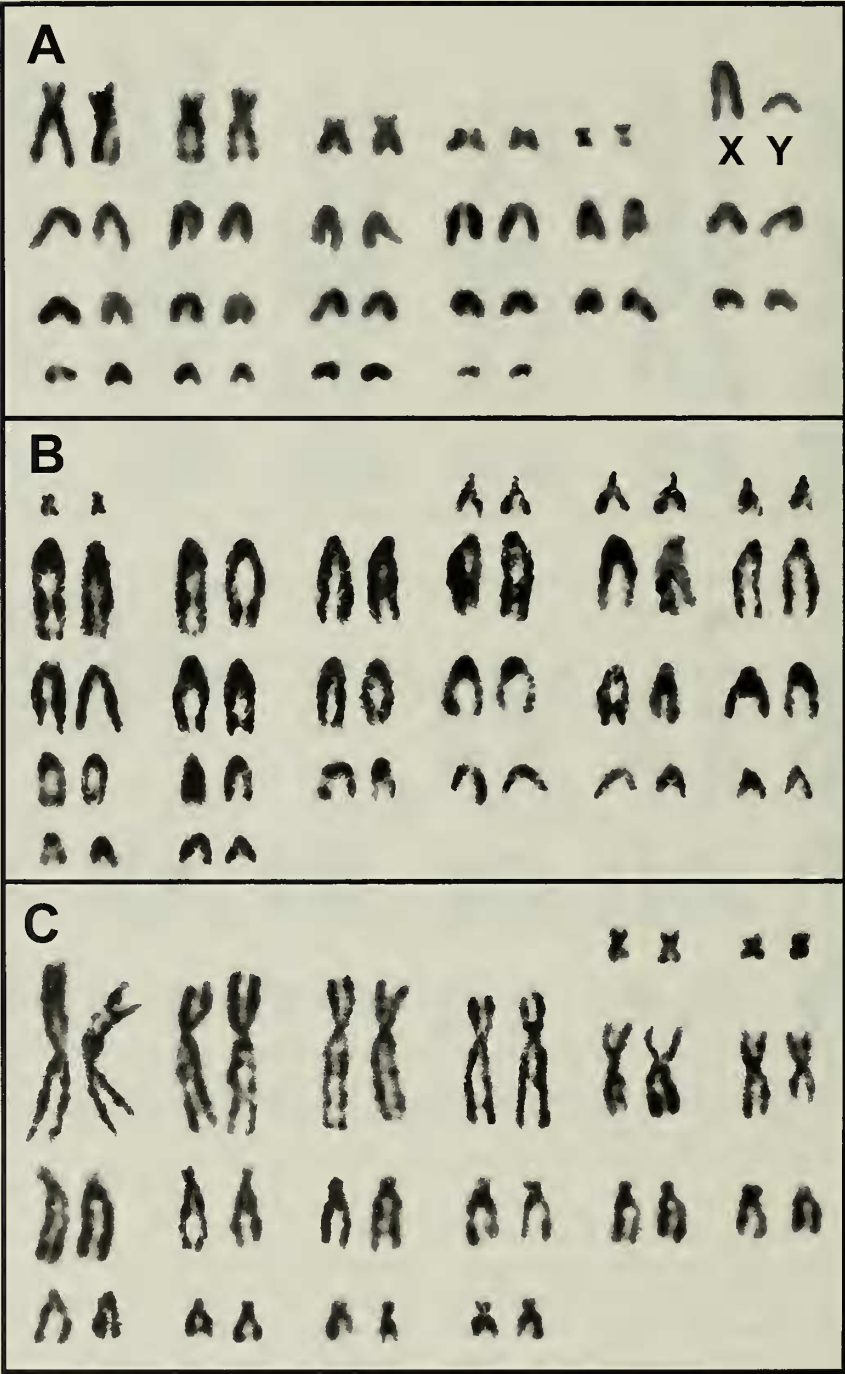


Fig. 5. Chromosomes of: A, *Apomys datae* male (FMNH 169051), 2N = 44, FN = 54; B, *Apomys hylocoetes* female (FMNH 147880), 2N = 48, FN = 56; C, *Apomys insignis* male (FMNH 147915), 2N = 36, FN = 72, in vitro preparation from a snap-trapped specimen. The sex chromosomes cannot be distinguished from the autosomes in these karyotypes.

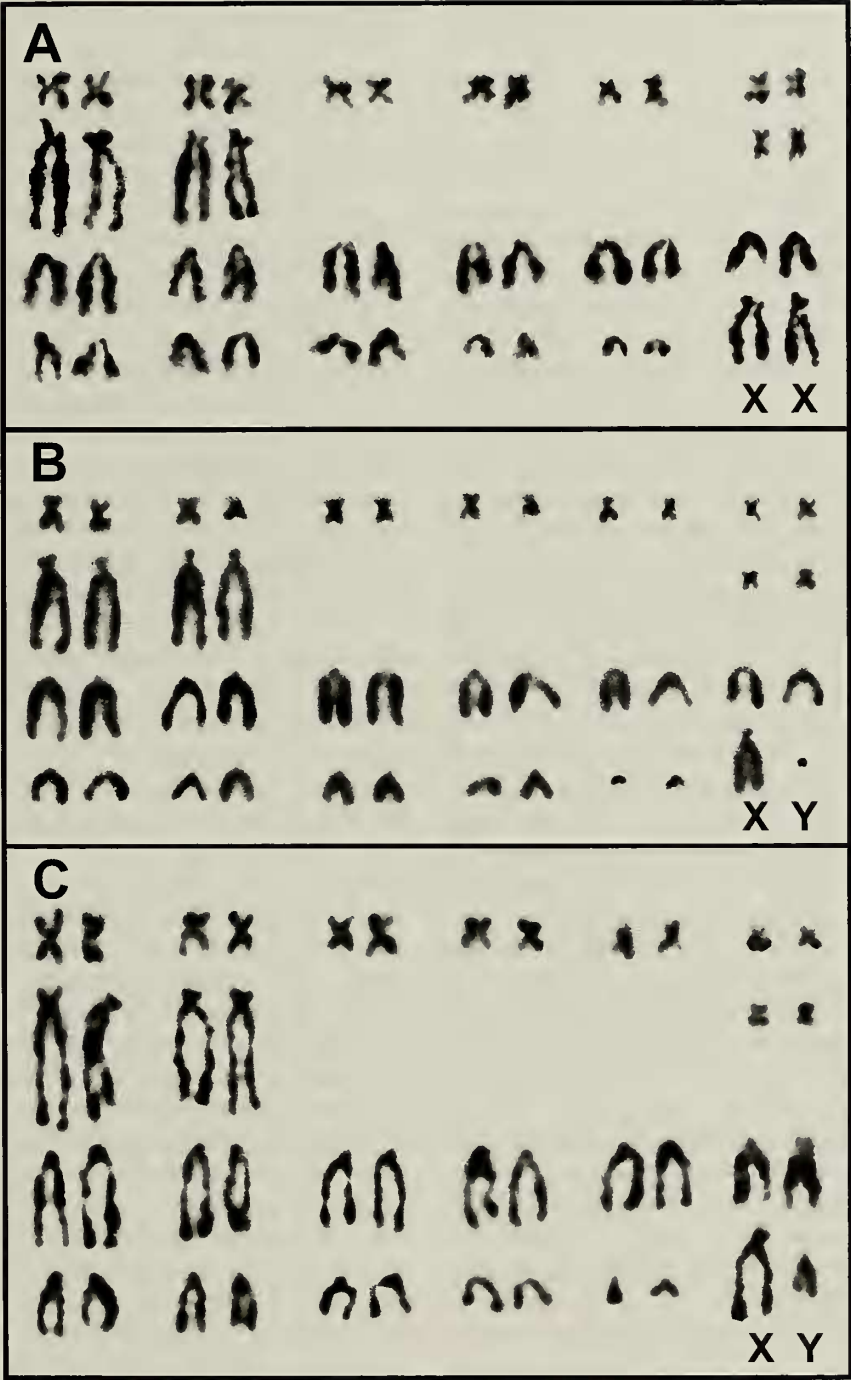


Fig. 6. Chromosomes of: A, *Linnomys sibuanus* female (FMNH 147943), 2N = 42, FN = 62, in vitro preparation from a snap-trapped specimen; B, *Linnomys* sp. male (FMNH 147975), 2N = 42, FN = 61; C, *Tarsomys apoensis* male (FMNH 147960), 2N = 42, FN = 61.

groups of genera and formulated alternative hypotheses regarding their potential phylogenetic relationships. Our discussion of chromosomal characteristics is framed within this context.

The genus *Phloeomys* includes two named species of large, arboreal, folivorous rats: *P. cumingi* from southern Luzon and adjacent islands of Catanduanes and Marinduque, and *P. pallidus* from central and northern Luzon (Heaney et al. 1998). Although *Phloeomys* is morphologically distinct from other Philippine murines, Musser & Heaney (1992) considered a relationship with the *Crateromys/Batomys* group as one alternative hypothesis. Based on non-differentially stained chromosomes, Rickart & Musser (1993) estimated a minimum of two Robertsonian and three non-Robertsonian events separating the karyotypes of *P. cumingi* ($2N = 44$, $FN = 66$) and *P. pallidus* ($2N = 40$, $FN = 60$). A comparison of the Giemsa-banded preparation from *P. cumingi* (Fig. 1) with published karyotypes of *P. pallidus* (Jotterand-Bellomo & Schauenberg 1988:183–184, figs. 2 & 3) reveal some additional differences. Although the preparations differ in the degree of chromosome condensation, the absence of any obvious arm homologies suggests that banding patterns have been altered through multiple non-Robertsonian events. The X chromosomes of the two species also appear to differ.

The arboreal and scansorial rats of the folivorous genera *Batomys*, *Carpomys*, and *Crateromys* are united by a suite of derived morphological features (Musser & Heaney 1992, Musser et al. 1998). Within this group, chromosomal data are available only for *Batomys granti* and *B. salomonseni*. Specimens from four population samples (two of each species) have indistinguishable standard karyotypes of 52 telocentric chromosomes (Rickart & Musser 1993:5, fig. 2). The high diploid number and predominance of telocentric elements in the *Batomys* karyotype are characteristics that have been considered primitive for murines (Viegas-

Pequignot et al. 1983, 1985). Although this has been accepted as a working hypothesis (Rickart & Musser 1993), there is no independent evidence to support it. The karyotype of *Batomys* and those of *Phloeomys* differ substantially, providing no support for a hypothesized close relationship between these groups of arboreal rats (Musser & Heaney 1992). *Batomys*, the shrew rats (Fig. 4; Rickart & Musser 1993:9, fig. 6), and *Apomys musculus* (Rickart & Musser 1993:6, fig. 3B), all have $FN = 52$. However, this resemblance may be entirely coincidental as there are no morphological characteristics that support a particularly close association of *Batomys* with these taxa (Musser & Heaney 1992).

The genus *Archboldomys* is endemic to Luzon Island and includes two named species, *A. luzonensis* and *A. musseri* (Musser 1982b, Rickart et al. 1998). Rickart & Musser (1993) reported the standard karyotype of *A. luzonensis* ($2N = 26$, $FN = 43$) and discussed an aberrant sex chromosome arrangement in that species. Three male specimens all have a karyotype that includes a large submetacentric X chromosome (the largest element in the complement) and a small telocentric Y chromosome. In Giemsa-banded preparations (Fig. 2A), the X chromosome appears similar to that of *Phloeomys* (Fig. 1). The faint banding on the long arm is probably the same pattern seen among many murines (Baverstock et al. 1983, Gadi & Sharma 1983, Jotterand-Bellomo & Schauenberg 1988). The other arm is apparently unbanded and heterochromatic, which also is common among murines (Baverstock et al. 1977, Gadi & Sharma 1983). The one available female specimen of *A. luzonensis* (which was phenotypically normal and pregnant when captured) is heterozygous for what appears to be an X chromosome deletion involving the loss of the heterochromatic arm (Fig. 2A, inset).

Information on the chromosomes of *Archboldomys musseri* is limited to a poor-quality in vitro preparation from one male specimen (Fig. 2B), but it is sufficient to

reveal substantial differences from *A. luzonensis*. Although the diploid number of 44 is an estimate, chromosome counts from multiple cells from this specimen were consistently greater than the $2N = 26$ of *A. luzonensis*, and there appear to be more telocentric elements. The relative size of the presumed X chromosome (the largest element) is the only clear similarity between the two karyotypes.

Archboldomys and *Crunomys* share features of external, cranial, and dental morphology, and have been considered close relatives (Musser 1982b, Musser & Heaney 1992). However, their similarities may represent shared primitive traits or simply reflect ecological convergence as relatively small, insectivorous "shrew-mice" (Rickart et al. 1998). Chromosomal data do not indicate a close relationship. *Crunomys suncoides* (Fig. 3A) resembles *A. luzonensis* in having a relatively low fundamental number compared to other endemic Philippine murines (Rickart & Musser 1993), but the entirely telocentric complement is considerably different from the *Archboldomys* karyotypes.

Aside from *Crunomys*, relatively few of the Asian murines that have been karyotyped have complements that are wholly telocentric (Rickart & Musser 1993:22, fig. 8). *Batomys* is the only other native Philippine murine that does, but it has a much higher diploid number than does *Crunomys*. Furthermore, the two genera have very dissimilar morphologies and are not thought to be closely related (Musser & Heaney 1992, Musser et al. 1998, Rickart et al. 1998). The standard karyotype of *Crunomys* most closely resembles those of *Cremnomys* from peninsular India ($2N = 36$; $FN = 36-37$; Gadi & Sharma 1983), but this may only be coincidental since there are no morphological features that link the two genera (Wroughton 1912, Rickart et al. 1998). Several species of *Mus*, including the commensal *M. musculus castaneus* (Fig. 3B), also have karyotypes consisting entirely or predominantly of telocentric elements, with

diploid numbers ranging from 26 to 48 (Rickart & Musser 1993:17, table 1). Furthermore, members of the Asian subgenus *Coelomys* also have "shrew-mouse" morphologies with external, cranial, and dental similarities to *Crunomys* (Marshall 1977, Musser & Newcomb 1983). As with *Archboldomys*, however, *Mus* (*Coelomys*) retains a primitive cephalic arterial pattern and has morphological specializations that distinguish it from *Crunomys* and may preclude a close relationship (Musser & Newcomb 1983, Musser & Heaney 1992).

The endemic genera *Chrotomys*, *Celaenomys*, and *Rhynchomys* include seven species of large-bodied Philippine "shrew-rats". Each has morphological specializations that reflect vermivorous habits (Rickart & Heaney 1991, Rickart et al. 1991, Musser & Heaney 1992, Heaney et al. 1999). The morphological differences between *Rhynchomys* and the other two genera are so distinct that Thomas (1895, 1898) placed them in different murid subfamilies. However, because they share many derived morphological traits, Musser and Heaney (1992) postulated monophyly of the three shrew-rat genera.

Chromosomally, the shrew-rats are a comparatively uniform group. The standard karyotype of *Celaenomys silaceus* (Fig. 4A) is identical to those of *Rhynchomys isarogensis* (as reanalyzed in this study) and *Chrotomys gonzalesi* (Rickart & Musser 1993:9, fig. 6). All have $2N = 44$, $FN = 52$, with two pairs of very small metacentric chromosomes, one pair of large submetacentric, a pair of large subtelocentric, and 18 pairs of telocentric chromosomes. Among Philippine murines with known karyotypes, this particular arrangement is unique to shrew-rats. The karyotype of *Chrotomys whiteheadi* ($2N = 38$, $FN = 52$; Fig. 4B) is distinctive within this otherwise chromosomally conservative group. It differs from the $2N = 44$ arrangement of *Celaenomys* and the other shrew-rats by three Robertsonian translocations, involving the substitution of three submetacentric chro-

mosome pairs for six pairs of telocentric elements.

Chromosomal evidence appears to support monophyly of shrew-rats. Furthermore, the distribution of karyotypes among the four species strongly suggests that the $2N = 38$ karyotype of *Chrotomys whiteheadi* is a novel arrangement derived through centric fusion from the $2N = 44$ karyotype.

With about 14 species, *Apomys* is the largest endemic genus of Philippine murines (Heaney et al. 1998). Chromosomally, it is also the most variable genus. Karyotypes are available for six species, each of which is unique (Figs. 5 & 6; Rickart & Musser 1993). Diploid and fundamental numbers range from 30 to 48, and from 50 to 88, respectively, indicating a variety of chromosomal rearrangements including both Robertsonian and non-Robertsonian events. The karyotype of *Apomys datae* ($2N = 44$, FN = 54; Fig. 5A) closely resembles that of *A. musculus* ($2N = 42$, FN = 52; Rickart & Musser 1993:6, fig. 3b). Both have similar diploid and fundamental numbers, include apparently homologous biarmed chromosome pairs, and have a predominance of telocentric elements.

Other *Apomys* species that have been karyotyped have arrangements that depart significant from those of *A. datae* and *A. musculus*. An undescribed species from Leyte Island (previously reported as *A. littoralis*) has a karyotype of $2N = 44$, FN = 88 (Rickart & Musser 1993:6, fig. 3a). It differs from *A. datae* by a series of non-Robertsonian events resulting in an entire complement of biarmed chromosomes. In contrast, the karyotype of an undescribed species from Negros Island with $2N = 30$, FN = 50 (Rickart & Musser 1993:7, fig. 4) represents a departure in a different direction, involving reduced diploid number and the loss of some chromosome arms.

Apomys hylocoetes and *A. insignis* are morphologically similar species that occur sympatrically on Mindanao Island (Musser 1982a). They have nearly identical cytochrome b sequences, and appear to be sis-

ter-species (Steppan et al. in prep.). Although closely related, these species exhibit major chromosomal differences. The karyotype of *Apomys hylocoetes* ($2N = 48$, FN = 56; Fig. 5B) consists predominantly of telocentric elements, whereas that of *Apomys insignis* ($2N = 36$, FN = 72; Fig. 5C) is composed entirely of biarmed elements. These arrangements differ from one another and from karyotypes of congeners by multiple events, both Robertsonian and non-Robertsonian.

The pattern of chromosomal variation within *Apomys* provides evidence of a close phylogenetic relationship with the shrew-rats, as hypothesized by Musser & Heaney (1993). In his review of the genus, Musser (1982a) separated *Apomys datae* from all other *Apomys* species based on its larger body size and pattern of cephalic arterial circulation. In both respects, it resembles the large shrew-rats (Musser & Heaney 1993). *Apomys datae* also is the most basal species in a molecular phylogeny of the genus (Steppan et al. in prep.). The close similarities between the karyotypes of *A. datae* (Fig. 5A), *A. musculus* (Rickart & Musser 1993), and the shrew-rats (Fig. 4), suggest that these arrangements are relatively primitive whereas those of other *Apomys* represent novel derivations in several different directions.

Limnomys and *Tarsomys*, together with *Abditomys*, *Tryphomys* and *Bullimus*, constitute a group of "new endemic" Philippine genera that share derived morphological features with the highly derived genus *Rattus*, and are phylogenetically distinct from other native Philippine murines (Musser & Heaney 1992). Available data demonstrate that this assemblage is chromosomally conservative. Standard karyotypes of *Bullimus* and *Rattus* (Rickart & Musser 1993) and of *Limnomys* and *Tarsomys* (Fig. 6) have $2N = 42$ and show little diversity in gross chromosome morphology. However, the Y chromosome is variable within this group. It is by far the smallest element in *Limnomys* (Fig. 6B), but is a substan-

tially larger telocentric element in both *Tarsomys* (Fig. 6C) and *Rattus everetti* (Rickart & Musser 1993:10, fig. 7B).

Of the 64 species of murine rodents known to occur in the Philippines (Heaney et al. 1998), karyotypes are available for 25 species in 13 genera (Jotterand-Bellomo & Schauenberg 1988; Rickart & Musser 1993; this report). These data reveal substantial chromosomal variation within the entire assemblage, and major differences in the apparent rate of chromosomal evolution within separate genera. *Batomys* and *Crunomys* have distinctive yet wholly telocentric karyotypes, arrangements that have been characterized as relatively primitive for murines (Viegas-Pequignot et al. 1983, 1985; Rickart & Musser 1993). *Phloeomys* and *Archboldomys* are chromosomally distinct from other murines, and both genera show substantial karyotypic variation at the species level. The chromosomal diversity of *Apomys* is remarkable, and includes major differences in the karyotypes of presumed sister-species.

The chromosomal data support two of the major phylogenetic hypotheses posed by Musser & Heaney (1992) based on their study of comparative morphology: (1) monophyly of the shrew-rat genera *Celaenomys*, *Chrotomys*, and *Rhynchomys*, and (2) a close relationship between the *Apomys* and the shrew-rats. The data also strongly support clustering of the endemic genera *Bullimus*, *Limnomys*, and *Tarsomys* with *Rattus* as a group distinct from other Philippine murines, but they provide no resolution within this cluster. Available data are not informative on the relationships of other Philippine genera.

Although standard karyotypes provide only limited insight into the phylogenetic relationships of Philippine murines, they have been extremely useful in clarifying taxonomic boundaries. Furthermore, the karyotype data reveal an emergent geographic pattern. Of the six endemic murine genera for which two or more species have been karyotyped (*Phloeomys*, *Batomys*,

Archboldomys, *Chrotomys*, *Apomys*, and *Tarsomys*), congeneric species have karyotypic differences in 14 of 16 comparisons. Of the two cases in which there are no noted differences, one (*Batomys*) involves species occurring in different faunal regions. In only one case (*Limnomys*) are species with similar standard karyotypes found in the same faunal region. The geographic patterning of chromosomal variation in murines resembles the more extensive pattern documented for Philippine bats (Rickart et al. 1999). The substantial differences observed among closely related taxa suggest that karyotypic change has been a causal factor in some speciation events.

Acknowledgments

We thank N. Antoque, D. Balete, R. Fernandez, G. Gee, S. Goodman, P. Heideman, J. Klompen, M. Lepiten-Tabao, B. Malaga, N. Mallari, D. Samson, D. Schmidt, A. Tabaranza, B. Tabaranza, L. Tag-at, and R. Utzurum for assistance in collecting specimens. E. King assisted with photomicrographs. Permits and logistical support were provided by the Philippine Protected Areas and Wildlife Bureau and the Philippine Bureau of Forest Development. Field work was supported by grants from the National Science Foundation (BSR 8514223), the John D. and Catherine T. MacArthur Foundation (90-09272A), and the Barbara Brown and Ellen Thorne Smith funds of the Field Museum.

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